

CYTOTAXONOMIC OBSERVATIONS ON
NORTH AMERICAN FERNS¹

WARREN H. WAGNER, JR.

DURING the last five years several contributions to our knowledge of the cytotaxonomy of North American ferns have been made. A list by Britton (1953) of thirty chromosome determinations of ferns collected in southern Ontario was followed by a report on the cytology of the *Dryopteris spinulosa* complex by Manton and Walker (1953), and later by a study of the Appalachian *Asplenium*s by the writer (1954). The present paper records a number of additional records based largely on plants of Michigan (Table I).

It seems desirable at this time to make a résumé (Table II) of our present knowledge of the chromosomes of North American ferns, and to point out, at least in some cases, where changes or modifications are suggested by the new evidence. The results thus far have yielded a number of taxonomic facts which may be expected to modify some of the concepts of relationship which have traditionally prevailed. A "progress report" pertaining to North American ferns is especially appropriate at this time since two important new revisions of northeastern American ferns have recently appeared, namely those of Gray's Manual of Botany, 8th ed. (Fernald, 1950), and the new Britton and Brown Illustrated Flora (Morton, *in* Gleason, 1952), two revisions which differ from each other quite significantly in a number of taxonomic interpretations and which thus strongly point up the need for new information. While groups of species in certain of our genera, such as *Dryopteris sens. str.* and *Asplenium*, form natural species complexes of considerable appeal to the cytotaxonomist, there are single, isolated species also, such as *Onoclea sensibilis* and *Pteretis pensylvanica*, which warrant attention because of their taxonomic interest at the generic and familial levels of classification. Of our sizeable species-groups, the knowledge of our native *Dryopteris*, *Asplenium*, and *Botrychium* species is being rapidly filled in. Notably absent, however, are data on such important and problematic indigenous assemblages as *Cheilanthes* and *Woodsia*. Of single, isolated

¹ This study was made possible by a Summer Faculty Research Fellowship awarded by the Horace H. Rackham School of Graduate Studies, University of Michigan.

species, there are certain ones which particularly invite study, notably such plants as *Lygodium palmatum*, *Pityrogramma triangularis* and its forms, and *Trichomanes boschianum*. That *Schizaea pusilla*, a disjunct species which occurs along the eastern seaboard, may have interesting cytological conditions is suggested by Selling's finding (1944) that its spores exist in two size groups.

Several of the most important types of evidence that have emerged from the study of chromosomes of ferns should be briefly mentioned. First, the data suggest that a given basic number will tend to be constant in large, related assemblages, and that "aneuploidy tends to characterize the relation between genera or groups of genera rather than between species." (Manton, 1950). For example, the *Asplenium* group apparently has a base number which is uniformly 36, while the two genera *Dryopteris* and *Polystichum* have 41, *Athyrium* has 40, and *Cystopteris* 42. Therefore, the determination of chromosome numbers may affect decisions concerning the validity of certain genera, such as *Gymnocarpium* which Morton maintained as distinct from *Dryopteris* but which Fernald did not. The general problem of generic interpretation in the assemblage formerly construed as belonging to one large genus "Dryopteris" has assumed special significance since Holttum's proposal that some of its elements may be so distinct as to represent a separate family, the Thelypteridaceae. This problem will be discussed further below. Another type of evidence possible from cytological studies of ferns bears on whether or not a given taxon is of hybrid origin. Such endemic plants as *Cystopteris fragilis* var. *simulans*, *Botrychium minganense*, and *B. oneidense* have certain seemingly intermediate morphological traits which lead one to suspect that they may have arisen by hybridization between other species. In sterile hybrids the behavior of the chromosomes at the time of spore production may sometimes lead to knowledge of their parents. In fertile hybrids, the chromosome complement may be double that of the parents, i.e., allopolyploids. A third type of evidence associated with chromosomes relates to the evaluation of subspecies or varieties. Thus Britton (op. cit.) has shown that the rare native American variety of the hart's-tongue fern, *Phyllitis scolopendrium* var.

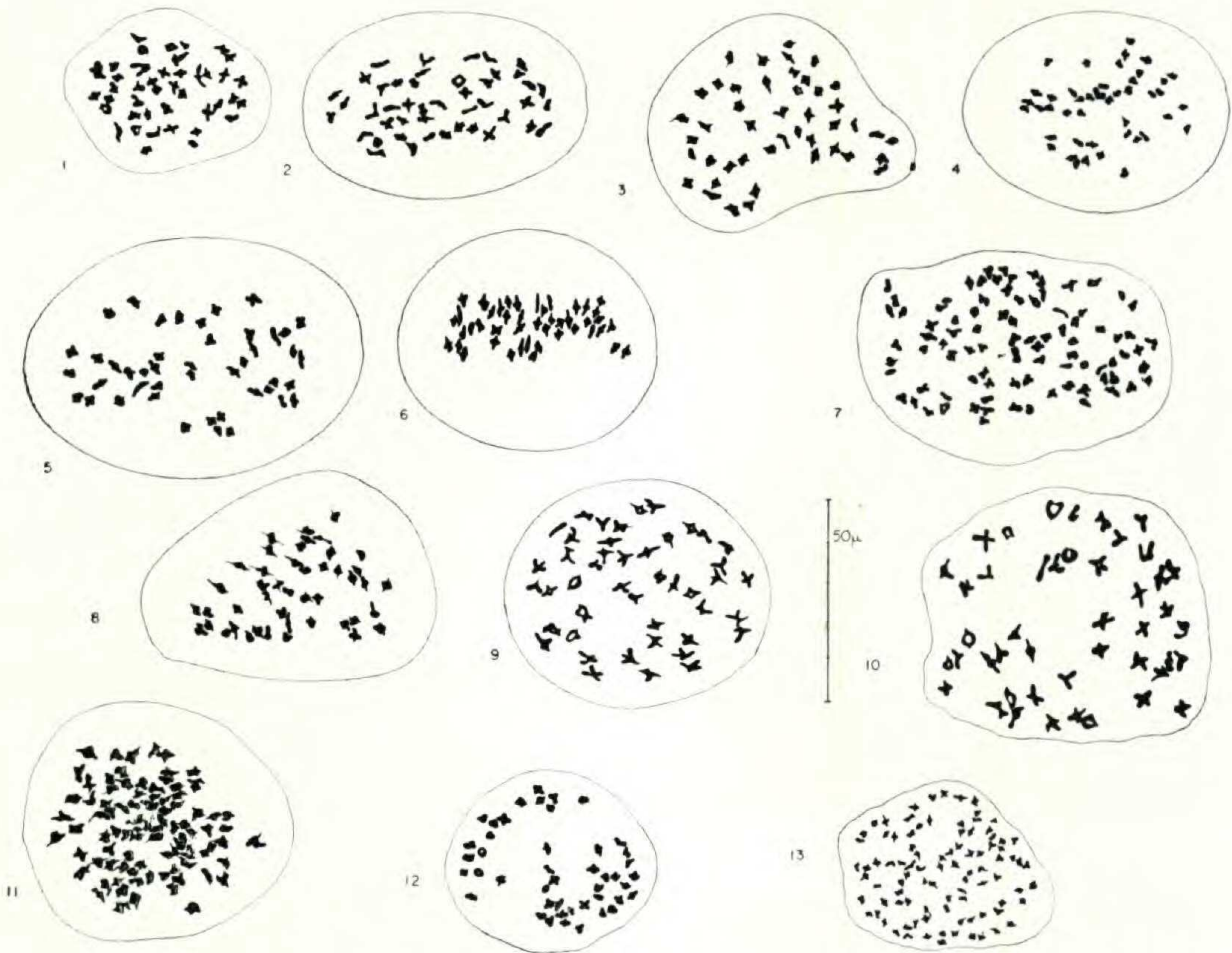


Fig. 1, *Botrychium multifidum*, Cheboygan Co., Mich. (Wiegand); Fig. 2, *B. multifidum*, Alpena Co., Mich.; Fig. 3, *B. oneidense*, Jackson Co., Mich.; Fig. 4, *B. oneidense*, Saginaw Co., Mich.; Fig. 5, *B. dissectum* f. *dissectum*, Saginaw Co., Mich.; Fig. 6, *B. dissectum* f. *obliquum*, Saginaw Co., Mich.; Fig. 7, *B. lunaria* var. *onondagense*, Emmet Co., Mich. (Voss); Fig. 8, *B. simplex* var. *tenebrosum*, Washtenaw Co., Mich.; Fig. 9, *B. simplex* var. *simplex*, Washtenaw Co., Mich.; Fig. 10, *B. pumicola*, Klamath Co., Oregon (R. D. Brown); Fig. 11, *B. matricariaefolium*, Livingston Co., Mich.; Fig. 12, *B. lanceolatum*, Emmet Co., Mich. (Voss); Fig. 13, *B. virginianum*, Washtenaw Co., Mich.

americanum, possesses the tetraploid condition, in contrast to the typical European plant which is a diploid.

I am indebted to a number of people for their interest and assistance in this project. In particular, I wish to acknowledge the expert help of Mr. Dale J. Hagenah, of the Cranbrook Institute of Science, who has contributed numerous living specimens for study, and Mr. Walter F. Kleinschmidt and the Staff of the Botanical Gardens of the University of Michigan, who have cultivated the living plants. Thanks are due also to those who supplied material, either fixed cytological specimens or living plants, unavailable in the immediate vicinity of Ann Arbor, including Mr. Donald F. M. Brown, Mr. Richard M.

Brown, Dr. Edward G. Voss, Miss Florence M. Wiegand, Dr. Edgar T. Wherry, and Dr. Carroll E. Wood.

METHODS: Leaflets or other fertile parts were collected in the field or in the greenhouse and put in Newcomer's solution (Newcomer, 1953) prior to squashing in aceto-orcein. Some of the earlier collections were fixed in a modification of Carnoy's solution (4 parts chloroform, 3 parts alcohol, 1 part glacial acetic acid). The results were essentially the same but the material seemed to last in a condition suitable for squashing for a longer period in Newcomer's solution. For members of the genus *Botrychium* it was desirable to crush and macerate masses of sporangia in the aceto-orcein on a microscope slide, and then to remove the large pieces of debris before adding the cover-slip. In addition, it was found effective to dry the outer surfaces of the *Botrychium* sporangia first before placing them in the stain, as this reduced the tendency toward precipitation. In all cases the top of the cover-slip was tapped with the point of a dissecting needle in order to spread out the sporocytes for pressing. The slide was heated nearly to boiling, and then pressed repeatedly with the forefinger on the surface of the cover-slip. In selecting cells to study, those which appeared to be intact, i.e., with unfragmented margins, were chosen. For each collection several perfect cells were carefully drawn with camera lucida at approximately 1450 times magnification using an oil-immersion objective, and a 15X widefield ocular. Using this technique, the size of the flattened cell cannot, of course, be controlled. However, those cells in which the chromosomes were most spread out were usually selected, although sometimes only slightly flattened cells showed chromosomes clearly and were used (cf. figs. 17 and 18). The voucher specimens are deposited in the Department of Botany, University of Michigan. They were made of the same plants or, in some cases, of plants from the same clone or colony, by mounting a leaf or leaves on herbarium sheets and pasting a camera lucida drawing of the chromosomes on the same sheet.

OBSERVATIONS: The genus *Botrychium* was the focus of considerable attention in this study because it was suspected that two of its species (*B. minganense* and *B. oneidense*) might be of hybrid origin. Although a number of species and varieties

are reported here for the first time, there still remain several taxa to be investigated. One of the primary difficulties in the study of *Botrychium* is in determining the time of meiosis in a given locality and, because of this, collections from a number of places turned out to be too far advanced in sporogenesis to be of any use in revealing chromosome numbers. Quite clearly in *Botrychium* the monoploid number is usually 45. *Botrychium virginianum* so far appears to be the only exceptional species, having an apparent base number of 46. This species has been found by Britton, in material from southern Ontario, and confirmed by the author from one locality in Michigan, to have a chromosome number of $n = 92$ (fig. 13). The chromosomes themselves appear to be conspicuously smaller than those of the other species of *Botrychium* examined. These cytological differences are interesting in view of the morphological features that characterize this species, such as the thin-textured blade, the partially exposed leaf primordium (the so-called "bud"), and the small sporangia. It will be profitable to determine whether the other members of the subgenus *Osmundopteris*, which, according to Clausen (1938), includes the native *B. virginianum* and four species of other parts of the world, will also reveal the base number 46.

In the subgenus *Sceptridium*, only two varieties of *B. dissectum* have been previously reported upon (Britton, 1953). The question of the related taxon, *B. oneidense* (Gilbert) House, has been an especially vexing one taxonomically since its original description by Gilbert around the turn of the century as a variety of "*Botrychium ternatum*." The latter epithet was used in the past to apply jointly to both *B. dissectum* and to *B. multifidum*, taxa now recognized as wholly distinct species by current authors. However, the plant in question, *B. oneidense*, is at present in the rather paradoxical situation of being interpreted by one author (Fernald, 1950) as a form of *B. dissectum* (*B. dissectum* forma *oneidense* (Gilbert) Clute), and by another (Morton, 1952) as a variety of the other species, *B. multifidum* (*B. multifidum* var. *oneidense* (Gilb.) Farwell). However, Fernald (op. cit., p. 21) describes the plant in question as being "embarrassingly transitional" between *B. dissectum* and *B. multifidum*; and Morton (p. 18) calls it "intermediate

TABLE I. CHROMOSOME NUMBERS⁴

Ophioglossaceae	
Botrychium multifidum (Gmel.) Rupr.	<i>n</i>
Levi Bur's farm, Cheboygan Co., Mich., June 26 (F. M. Wiegand)...	45
Williams Lake Rd., Oakland Co., Mich., June 19.....	45
Sharon Hollow, Washtenaw Co., Mich., June 22.....	45
Lime sinks near Leer, Alpena Co., Mich., July 3 (D. J. Hagenah)...	45
B. oneidense (Gilbert) House	
Waterloo-Munith Rd., Jackson Co., Mich., July 18.....	45
Jackson Rd., s. of Chelsea, Washtenaw Co., Mich., July 30.....	45
S of Frankenmuth, Saginaw Co., Mich., July 31.....	45
B. dissectum Spreng. f. obliquum (Muhl.) Fern.	
U. of Mich. Arboretum, Ann Arbor, Washtenaw Co., Mich., July....	45
S of Frankenmuth, Saginaw Co., Mich., July 31.....	45
B. dissectum Spreng. f. dissectum	
S of Frankenmuth, Saginaw Co., Mich., July 31.....	45
B. lunaria (L.) Sw. var. onondagense (Underw.) Clute	
Mackinaw City, Emmet Co., Mich., May 15 (E. G. Voss).....	ca. 90
B. simplex E. Hitch. var. tenebrosum (A. A. Eat.) Clausen	
Mud Lake, Washtenaw Co., Mich., May 10.....	45
B. simplex E. Hitch. (typical)	
Silver Hill Rd., near hdqtrs., Pinkney Area, Washt. Co., May 14....	45
Oakwood Rd., near Sashabow Rd., Oakland Co., Mich., June 19....	ca. 45
B. pumicola Coville	
Llao Rock, Crater Lake, Klamath Co., Oregon, June 19 (R. D. Brown)	45
B. matricariaefolium A. Br.	
2 mi. w. of Howell, Livingston Co., Mich., May 7.....	ca. 90
Silver Hill Rd., near hdqtrs., Pinkney Area, Washt. C., May 14....	ca. 90
Maple River Twp., Emmet Co., Mich., May 15 (E. G. Voss).....	ca. 90
B. lanceolatum (Gmel.) Angst. ssp. angustisegmentum (P. & M.) Clausen	
Maple River Twp., Emmett Co., Mich., May 15 (E. G. Voss).....	45
B. virginianum (L.) Sw.	
Hankerd Rd., Pinkney Area, Washtenaw Co., Mich., May 15.....	92
"Polypodiaceae"	
Pteridium aquilinum (L.) Kuhn var. pseudocaudatum (Clute) Heller	
1.5 mi. s. of Lillington on Route 15A, Harnett Co., N. C., gh, July 28 (C. E. Wood).....	52
Onoclea sensibilis L.	
Jackson Rd., s. of Chelsea, Washtenaw Co., Mich., July 29.....	37
Cystopteris bulbifera (L.) Bernh.	
Paint Creek, Ross Co., Ohio, gh, Sept. 5 (D. F. M. Brown).....	42
Oxford 40, Oakland Co., Mich., June 17.....	42
C. fragilis (L.) Bernh.	
Lake Michigamme, Marquette Co., Mich., gh, April (D. J. Hagenah)	84
Grand Ledge, Eaton Co., Mich., gh, May 16 (D. F. M. Brown)....	84
C. dickiana Sim	
Mt. Bohemia, Keweenaw Co., Mich., gh, July 19 (D. J. Hagenah)...	84
C. fragilis var. tennesseensis (Shaver) McGregor	
Fayette, Delta Co., Mich., gh, July 19, 20 (D. J. Hagenah).....	126
Trout Lake, Chippewa Co., Mich., gh, Aug. 13 (D. J. Hagenah)....	126
C. fragilis var. simulans (Weatherby) McGregor	
Catoctin Furnace, Frederick Co., Md., gh, June 17 (E. T. Wherry) ca.	84
Bernville, Berks Co., Penn., gh, July 26 (E. T. Wherry).....	84
Thelypteris (Phegopteris) hexagonoptera (Michx.) Weatherby	
Sharon Hollow, Washtenaw Co., Mich., June 22.....	30
Pine Lake, Hope Twp., Berry Co., Mich., June 25 (D. J. Hagenah)...	30
Jackson Rd., s. of Chelsea, Washtenaw Co., Mich., July 4.....	30

⁴ Where chromosome determinations were made from materials grown in the greenhouse, the date of meiosis is probably not significant, so those cases where greenhouse plants were used are indicated by "gh".

TABLE I.—Continued

T. noveboracensis (L.) Nieuwl.	
Waterloo-Munith Rd., Jackson Co., Mich., June 25.....	27
Fodunk, Barry Co., Mich., June 29 (D. J. Hagenah).....	27
Jackson Rd., s. of Chelsea, Washtenaw Co., Mich., July 4.....	27
Proud Lake, Oakland Co., Mich., July 11.....	27
T. palustris Schott. var. pubescens (Lawson) Fern.	
M92, near Green Lake, Waterloo Area, Washt. Co., Mich., July 16..	35
Athyrium filix-femina (L.) Roth var. michauxii Mett.	
Sharon Hollow, Washtenaw Co., Mich., July 2.....	40
A. thelypteroides (Michx.) Desv.	
Sharon Hollow, Washtenaw Co., Mich., July 2.....	40
Jackson Rd., s. of Chelsea, Washtenaw Co., Mich., July 4.....	40
A. pycnocarpon (Spreng.) Tidestr.	
Sharon Hollow, Washtenaw Co., Mich., August 3.....	40
Woodwardia (Anchistea) virginica (L.) Sm.	
Mud Lake, Washtenaw Co., Mich., July 10.....	35
Near Stockbridge, Ingham Co., Mich., July 13.....	35
Olson, Midland Co., Mich., July 31.....	35
W. (Lorinseria) areolata (L.) Moore	
Eastern North Carolina (plant in U. of N. C. greenhouse), Aug. 15	
(C. E. Wood).....	35
Asplenium ruta-muraria L. var. cryptolepis (Fern.) Wherry	
Sunfish Creek, Pike Co., Ohio, gh, May 23 (D. F. M. Brown).....	72

between *B. multifidum* . . . and *B. dissectum* var. *obliquum* and possibly a hybrid between them." Obviously it was especially desirable to determine whether or not there was cytological evidence of hybridity in the presumed intermediate.

To this end, materials of *B. multifidum* were studied from four different counties of Michigan, of *B. oneidense* from three counties, and of *B. dissectum* from two counties. For all three of the basic taxa under discussion the chromosome number proved to be $n = 45$, as determined in meiosis. There was no evidence of hybridity, either in irregular pairing or polyploidy, in the materials of *B. oneidense* which were unquestionably typical of this taxon (cf. figs. 1-6). For this reason, and because of numerous field observations which Mr. Hagenah and the writer have made of the members of this complex in the field, I believe that *B. oneidense* merits interpretation as a distinct species, and that the current concepts of this entity (a) as a variety or form of *B. dissectum*, (b) as a variety or form of *B. multifidum*, or (c) as a hybrid between them, may be erroneous. The hybrid hypothesis especially does not seem to be supported by cytological evidence. Furthermore, all three entities have been found to co-exist in the same locality without evidence of intergradation and the presumed "intermediate" does not seem really to be intermediate. It is hoped that in the near

future a detailed analysis of the problem of *B. oneidense* can be presented.

In the subgenus *Eubotrychium*, only the European form of *Botrychium lunaria* has been reported (Manton, op. cit., $n = 45$). In North America, the major taxonomic problem involving this subgenus appears to the writer to be the plant described as *B. minganense* Victorin, which was treated by subsequent authors as merely a variety or form of *B. lunaria*. Although its author described it as a distinct species, Clausen (1938) reduced it to varietal status under *B. lunaria*, stating (p. 68) that "collections from Michigan, Alberta, and various places in the Rocky mountains indicate that, at least in those areas, a complete transition occurs." Morton (1952) also interprets *B. minganense* as a variety of *B. lunaria*, and writes (p. 16) that it is "scarcely distinguishable from the typical variety" of *B. lunaria*; Fernald (1950, p. 22) treats it simply as a form.

Our interest in *B. minganense* has become heightened by a number of field studies which indicate that the Michigan representative is clearly a distinct entity, capable of living sympatrically with typical *B. lunaria* and entirely without transition. In some respects it appears to be intermediate between *B. lunaria* and *B. matricariaefolium*. Although we are still unable to report a chromosome count in *B. minganense*, its spores have been reported to be larger than those of *B. lunaria*, suggesting that it may be a polyploid. However, the latter possibility is complicated now by the fact that the single population of *B. lunaria* which has been studied turned out to be a polyploid itself, with approximately 90 pairs of chromosomes at meiosis. It should be emphasized in this case that the material, from Emmet Co., Mich., represents the endemic variety, *B. lunaria* var. *onondagense*, and material wholly typical of *B. lunaria* from North America has not yet been examined. The problem of chromosome numbers in the *B. lunaria* group is therefore recommended to workers in various places in the area of occurrence of these taxa, roughly from Labrador to Alaska and California, east to northern Wisconsin and Michigan. *B. matricariaefolium* has yielded approximately 90 pairs of chromosomes in the three populations examined, so it is polyploid like *B. lunaria* var. *onondagense*.

The two extreme varieties of *Botrychium simplex* which occur most commonly in Michigan have such different habitats and aspects that it was suspected that they might prove to be different cytologically. *Botrychium simplex* var. *tenebrosus* is normally a plant of deep shady woods in swamps, whereas *B. simplex* of the typical variety occurs usually in open fields on hillsides in relatively dry habitats. Cytologically, however, the two varieties proved to be indistinguishable (figs. 8 and 9). The closely related *B. pumicola*, a rare and local species known only from a couple of localities in Oregon and California, was found also to be like typical diploid Eubotrychiums in its cytology (fig. 10).

Eubotrychium sect. *Lanceolatae* Clausen comprises a single species, *B. lanceolatum*, which is represented in the northeastern United States primarily by its variety *angustisegmentum*. Specimens of the latter from Emmet Co., Michigan, showed chromosome complements which were indistinguishable from those of members of Subgenus *Sceptridium* and Sect. *Lunariae* (fig. 12).

ONOCLEA: The genus *Onoclea* is monotypic and its single species, *O. sensibilis*, occurs both in eastern North America and in eastern Asia. In morphology it is a unique genus and the generic relationships are not clear, although, as pointed out by Britton (op. cit), it has been placed in close proximity to *Pteretis*. This interpretation rests largely on the fact that the sporangia are produced on much-modified fertile fronds. Britton has found $n = 37$ in Canadian plants, with a possible error in interpretation of not more than one bivalent. The writer determined 37 pairs in clear preparations of material from Washtenaw Co., Mich., thus adding more certainty to this number. The large-sized chromosomes of *Onoclea* are distinctive, and Fig. 15 shows a cell which is only slightly flattened and in which the chromosomes themselves have apparently not been flattened at all. Britton points out that since the chromosome number of *Pteretis pensylvanica* is 40, the plants are probably not closely related. Research on the comparative morphology and anatomy of these two genera is strongly recommended, to see especially whether they might have acquired their similar-appearing fertile fronds through parallel evolution from unrelated ancestors in which the fronds are monomorphic.

PTERIDIUM: Typical plants of *Pteridium aquilinum* (L.) Kuhn from Europe were determined by Manton to have a chromosome number of $n = 52$. More recently Britton has reported that the eastern American var. *latiusculum* (Desv.) Underw. has this number likewise; and in the present study a plant of *P. aquilinum* var. *pseudocaudatum* (Clute) Heller collected by Dr. Carroll E. Wood, Jr. near Lillington, N. C., was found also to have $n = 52$ (fig. 14).

CYSTOPTERIS: Some years ago, Mr. Weatherby (1935) discussed the forms of the *Cystopteris fragilis* complex in eastern North America, and he showed that there are a number of distinct varieties, including a taxon he described as forma *simulans* Weath., with leaf cutting like *C. bulbifera*. Since that time two rather important findings have been made: (1) A peculiar "bulblet-bearing" plant which evidently combines characters of *C. fragilis* and *C. bulbifera* has been reported from a very wide area of Kansas to Pennsylvania and the southern shore of Lake Superior (the last localities discovered by D. J. Hagenah and as yet not reported in detail). Bulblet-bearing plants were named *C. tennesseensis* by Shaver (1950) and plants somewhat like them had been reported earlier by Wherry (1944) and Wagner (1944). Since then, McGregor (1950) has reduced *C. tennesseensis* to varietal status under *C. fragilis*, and he points out that it differs from var. *simulans* (Weath.) McGregor primarily in having minute white glands and narrower pinnae. It is now known that both forms have "bulblets" along the rachis and occasionally along the costae of the pinnae, although var. *simulans* commonly lacks them. All the authors concerned with the relationships of these plants in recent years have suggested hybridity, especially on the basis of the "bulblets" (which, however, are morphologically quite different from those of *C. bulbifera*)². (2) The second recent discovery involves an overlooked American fern, *Cystopteris dickieana* Sim. It has now been recorded from a number of localities where it had previously been undetected because of the microscopic nature

² The first mention of bulblets in *Cystopteris fragilis* that I have found is by Pinkerton, M. Elizabeth, 1933, Ferns and Fern Allies of Missouri, Ann. Missouri Bot. Gard, 20: 45-78, who writes (p. 59) under *C. fragilis*, "An exceedingly variable species. Hybridization with *C. bulbifera* might account for some of the aberrations. Forms bearing bulblets have been included under this group as that character does not seem to be a constant feature for *C. bulbifera* alone."

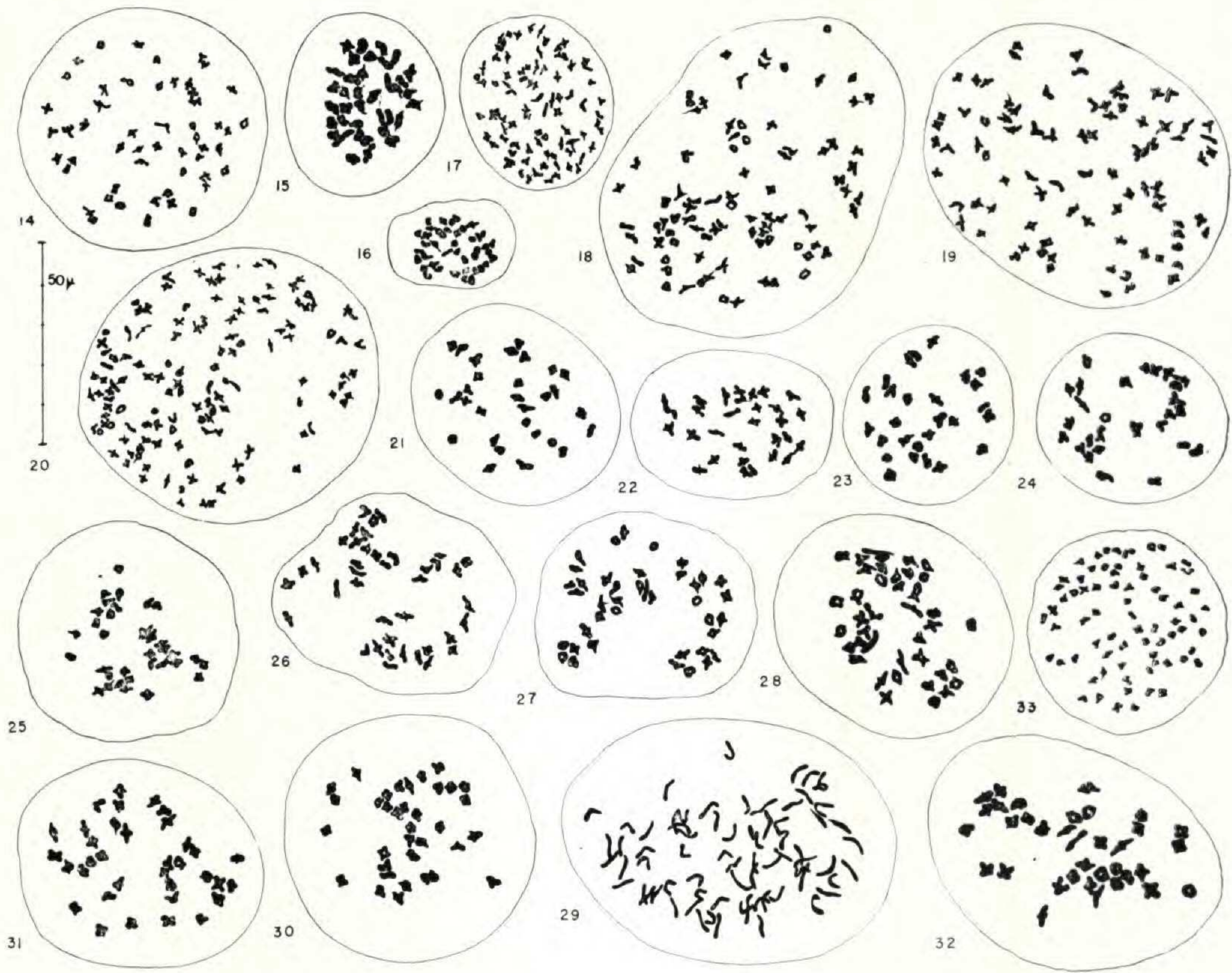


Fig. 14, *Pteridium aquilinum* var. *pseudocaudatum*, Harnett Co., N. C. Note: this figure is drawn at approximately two-thirds the magnification of the others, and is not to scale. (C. E. Wood); Fig. 15, *Onoclea sensibilis*, Washtenaw Co., Mich.; Fig. 16, *Cystopteris bulbifera*, Ross Co., Ohio (D. F. M. Brown); Fig. 17, *C. fragilis*, Eaton Co., Mich. (D. F. M. Brown); Fig. 18, *C. dickieana*, Keweenaw Co., Mich. (D. J. Hagenah); Fig. 19, *C. fragilis* var. *simulans*, Berks Co., Penn. (E. T. Wherry); Fig. 20, *C. fragilis* var. *tennesseensis*, Delta Co., Mich. (D. J. Hagenah); Fig. 21, *Thelypteris hexagonoptera*, Washtenaw Co., Mich.; Fig. 22, *T. hexagonoptera*, Barry Co., Mich. (D. J. Hagenah); Fig. 23, *T. noveboracensis*, Jackson Co., Mich.; Fig. 24, *T. novaboracensis*, Oakland Co., Mich.; Fig. 25, *T. palustris* var. *pubescens*, Washtenaw Co., Mich.; Fig. 26, *Athyrium filix-femina* var. *michauxii*, Washtenaw Co., Mich.; Fig. 27, *A. thelypteroides*, Washtenaw Co., Mich.; Fig. 28, *A. pycnocarpon*, Washtenaw Co., Mich.; Fig. 29, *Woodwardia virginica*, Washtenaw Co., Mich. (somatic division); Fig. 30, the same (meiotic division); Fig. 31, *W. virginica*, Ingham Co., Mich.; Fig. 32, *W. areolata*, U. of North Carolina greenhouse (C. E. Wood); Fig. 33, *Asplenium ruta-muraria*, Pike Co., Ohio (D. F. M. Brown).

of its distinction from typical *C. fragilis*. It differs from the latter species in its spores which are rugose (like those of *Woodsia*, for example) while those of *C. fragilis* are echinate (Alston, 1950). The cytological data to be presented here should be expanded considerably before we may consider our understanding of North American *Cystopteris* to be complete from this standpoint.

However, one point emerges clearly in connection with the

presumed hybrids of *Cystopteris* which now favors McGregor's varietal interpretation of the taxa in the "hybrid" group. Cytological studies of *C. fragilis* in Europe and in North America (the latter including the reports of $n = 84$ by Britton and the present writer, fig. 17) show that there is so far no evidence of a low number of 42, such as that found in *C. bulbifera* in material from southern Ontario and from Michigan and Ohio (fig. 16). The European typical *C. fragilis* not only occurs in tetraploid races, but in hexaploid as well. In North America only the tetraploids have been found. A fertile hybrid of *Cystopteris bulbifera* and *C. fragilis*, whether allopolyploid or apogamous, would probably be expected to show at least the hexaploid condition of 126 pairs at meiosis, combining the 84 pairs of *C. fragilis* with the 42 of *C. bulbifera*. But such was not the case in plants that show the "hybrid" characteristics and which conform to McGregor's concept of var. *simulans* collected by Dr. Wherry at Bernville, Berks Co., Pa. (fig. 19) where the number is $n = 84$. In plants like the foregoing from Catoctin Furnace, Frederick Co., Md., the precise number has not been yet determined but it is certainly not more than two bivalents different from 84 pairs. Accordingly, at least two populations do not readily conform to a hybrid hypothesis based on current knowledge of the cytology of the two putative parents as they occur in North America.³ On the other hand, similar "bulblet-bearing" materials from Fayette, Delta Co., and from Trout Lake, Chippewa Co., Michigan, which fit McGregor's interpretation of var. *tennesseensis* in having many delicate glands on the leaf surfaces have yielded the hexaploid number of chromosomes, showing clearly in a number of preparations 126 pairs at meiosis. The latter are the first reports of hexaploids in the genus as it occurs in North America. The fact that the "hybrids" show two numbers now complicates

³ The possibility should be recognized, however, that there might exist *now* or might have existed *at some time in the past* more primitive populations of *Cystopteris fragilis* in which the chromosome number was diploid. Thus var. *simulans*, it might be argued, could have arisen from the hybridization of *C. bulbifera* and a diploid *C. fragilis*, and var. *tennesseensis* arose from *C. bulbifera* and a tetraploid *C. fragilis*. (The fact that hexaploids are known in European *C. fragilis* indicates that almost surely there were at one time, at least, diploids in that species.) The wide ranges now known in the "hybrids" make it reasonable that they could have originated in ancient times. The point is that we do not—at present—have direct evidence of diploid *C. fragilis* in any known North American populations.

the picture, but McGregor's interpretation of the "hybrid" plants as comprising two taxa seems to be substantiated.

Of *C. dickieana*, only one population has thus far been studied in North America and this, like the European plants of the same taxon studied by Manton (op. cit., pp. 117–120), yielded $n = 84$ (fig. 18). In the writer's opinion the taxonomic treatment of this plant as a species should be questioned, since up to now I am not aware that it has been shown to differ in more than a single reliable character from *C. fragilis*. It is even conceivable that the difference between rugose and echinate spores in this case depends on merely one or a few genes.

DRYOPTERIS sens. lat.: One of the major taxonomic problems in filicinean classification in general is the proper disposition of the generic groups formerly associated with *Dryopteris* in the broad sense, as illustrated locally by Fernald's treatment (1950, pp. 31–37) which includes widely divergent plants. He states, however, that *Dryopteris* (s.l.) is a "large and very complex world-wide genus, its sections by some considered to form genera." Morton (1952, pp. 48–55) considered the eastern North American species as belonging to three genera, viz. *Thelypteris* (syn. *Lastrea* of Copeland, 1947), *Gymnocarpium*, and *Dryopteris* s.s., and he has given his reasons for this interpretation elsewhere (Morton, 1950, pp. 214–218). The most radical treatment of the generic groups is that of R. E. Holttum (1946, pp. 130–133) mentioned above, in which the *Thelypteris* group is interpreted as a distinct family, *Thelypteridaceae*, demarcated from the *Dryopteris* s. s. group which he deals with as a subfamily (Dryopteridoideae) of his Dennstaedtiaceae. Such a seemingly "violent" interpretation will no doubt surprise many taxonomists versed in traditional fern classification, but the cytological evidence accumulated thus far appears indeed to warrant a sharp division of some sort between these generic groups. Manton has recently concluded (1954, pp. 16–17) that "there is very clear evidence that Copeland's Aspidiaceae is polyphyletic at least to the extent that the *Thelypteris* group of genera with $n = 31, 34, 35,$ and $36,$ are wholly discordant, the rest of the 'family' being all based on $40, 41,$ or $42.$ Holttum's new family of Thelypteridaceae is therefore strongly supported." With this in mind, the comments in the following

discussion will be divided into two parts, the first concerning the *Thelypteris* group and the second the *Dryopteris* group.

The chromosome number of the North American representative of the type species of *Thelypteris* (*T. palustris* var. *pubescens* (Lawson) Fernald) has been reported as $n = 35$ by Britton in Canadian material, and is confirmed by the writer on material from Washtenaw Co., Michigan (fig. 25). The two new numbers to be reported here in the *Thelypteris* group are of special interest, including one which establishes the base number of the segregate *Phegopteris* for the first time, and another which is lower than any previously reported.

The "broad beech fern," *Thelypteris* (*Phegopteris*) *hexagonoptera* (Michx.) Slosson is an endemic North American species ranging from Quebec and Minnesota south to Florida and Texas. It is closely related to *T. phegopteris* (L.) Slosson, the "northern" or "narrow beech fern," a circumboreal species which has been found to be apogamous and to possess 90 pairs of chromosomes at meiosis in British plants studied by Manton and in Canadian plants studied by Britton. Both of the species under discussion have also been placed in a separate genus, *Phegopteris*. With regard to the widespread northern species, Manton wrote (1950, p. 184) that "The possible origin of the species . . . is at present unknown, since the chromosome number (90) is unlike that of any of the genera with which *Phegopteris* has from time to time been classed, and there is therefore no clue to its nearest affinities." It was found that the majority of sporangia of this species show only 8 spore mother cells, instead of the usual 16, and that both generations possess 90 chromosomes, thus indicating the apogamous type of life-cycle.

It is therefore extremely interesting to report that three populations of the endemic American species, *T. hexagonoptera*, were found to possess only 30 pairs of chromosomes at meiosis (figs. 21, 22). This new number suggests (a) that 30 is probably the original, basic number for this pair of species (i. e., for *Phegopteris* as a segregate genus or subgenus), (b) that *T. hexagonoptera* very likely has the more primitive, sexual type of life-cycle, and (c) that there is some justification from the cytological evidence for upholding *Phegopteris* as a distinct genus.

The chromosomes of the "New York fern," *Thelypteris noveboracensis* (L.) Nieuwland were examined because Britton (op. cit., p. 577) indicated that it was a difficult species to study and reported the number of $n = 29 \pm 2$ only for interest and as a tentative determination. Because also of the divergence of this tentative number from the previously reported ones of 31, 34, 35, and 36, it seemed desirable to examine several populations, and the results that emerged in this investigation (figs. 23, 24) turned out to be even more divergent than had been expected. The chromosome number of *T. noveboracensis* appears to be unique— $n = 27$. The chromosome number range now known in the *Thelypteris* group—from 27 to 36—indicates either that within this assemblage the generalization that chromosome numbers are more or less uniform for related groups at the level of genus does not apply here, or that the *Thelypteris* group is polyphyletic, and its members are perhaps less closely related phylogenetically than had been supposed.

In the group of *Dryopteris* sens. str., it is now well known that the basic number of chromosomes of $n = 41$ is quite different from the numbers known in the *Thelypteris* group with the possible exception of *Thelypteris* (*Gymnocarpium*) *dryopteris* and *T. (G.) robertianum*. The primary cytotaxonomic interest of *Dryopteris* in North America concerns the degree of hybridization which has played a role in the evolution of the species. It should be stressed that to a considerable extent authors have seemingly underestimated the degree to which hybridization has occurred within this genus in eastern North America: practically no large "woodfern" swamp is lacking in numerous intermediate individuals which the critical plant collector will inevitably notice, and which often provide "headaches" in identification. Furthermore, these plants which are certainly of hybrid origin are apomictic, and are capable over a period of years of forming populations by vegetative reproduction. Spread of the plants is accomplished by small buds which develop, several at a time, at the bases of the withering petioles in the autumn, and these are capable of forming successive "families" of plants around old individuals. As it stands, there is no really thorough-going source for determination of these intermediate plants in the herbarium, nor, in fact, has it been until

very recently that convincing cytological evidence for their hybridity has appeared. The attention of pteridologists is called to the important work of Manton and Walker (1953), not yet completed, which is of major interest to students of this group.

ATHYRIUM: In tropical areas the genus *Athyrium* often constitutes a bewildering assemblage taxonomically; in North America, however, there are but few species and the major problems are at the subspecific level. Such taxonomic work as has been done on this group has been largely of a subjective nature and little detailed knowledge of the plants concerned is available. Intensive investigations are much needed, especially among the indigenous forms of the *Athyrium filix-femina* complex, which includes at least several distinctive subspecies or varieties, and a large number of forms. Until now, only typical *A. filix-femina* from Britain has been reported ($n = 40$), and *A. filix-femina* var. *michauxii* Mett. (syn. *A. angustum* Small) from southern Ontario and Michigan (with the same number).

Of other North American indigenous species of *Athyrium* there are no previous records. *Athyrium thelypteroides* (Michx.) Desv. from two localities in Washtenaw Co., Michigan, yielded $n = 40$. The most distinctive of the native species, *A. pycnocarpon* (Spreng.) Tidestr., of which Morton (1952, p. 43) wrote "This species is of uncertain generic relationships," also showed $n = 40$. There thus appears to be no special evidence from chromosome number to support placing *A. pycnocarpon* in a separate genus (e.g., as *Diplazium pycnocarpon* Broun, or *Homolosorus* Small). It is interesting to observe that meiosis occurred fully a month later (early August) in *A. pycnocarpon* than it did in the two other species which were found growing with it in the same locality. In *A. pycnocarpon* there were not even crosiers of fertile fronds evident above the ground level at the time fully formed fertile fronds of *A. filix-femina* and *A. thelypteroides* were collected in early July.

WOODWARDIA: Britton (op cit., p. 577) wrote of the Virginia chainfern, *Woodwardia (Anchistea) virginica*, that the chromosome number was $n = 36$, and that "this chromosome number may indicate an affinity between this genus and *Asplenium*."

(Such a relationship was suggested earlier by Bower and other authors on what seemed to be morphological resemblances.) Because of this interesting apparent correlation, and the ready availability of this species in southern Michigan, three populations were studied. Meiotic figures were observed in all three, and in one population mitotic figures of archesporial cells were also studied. The results differ from those of Britton: in all three cases there was no doubt that the gametic number is 35. (In a couple of sporocytes, two unpaired univalents were clearly observed, suggesting an occasional early separation of one of the bivalents at the time of metaphase, but otherwise in the numerous cells examined there was no question concerning the number.) Britton indicated in his count, however, a possible error of ± 1 . The present number of 35 does not so evidently suggest a relationship of *Woodwardia* to *Asplenium*.

Toward the end of this investigation, Dr. Wood kindly sent materials of the very different-appearing species, *Woodwardia* (*Lorinseria*) *areolata*, from living plants in the University of North Carolina greenhouse. It had been expected that this species might perhaps prove to have a different chromosome number, especially in view of the fact that the number $n = 34$ is now known in Old World species of *Blechnum* and *Woodwardia*. However, it turned out that *W. areolata* has the same number as *W. virginica*, $n = 35$ (fig. 32), and there is, therefore, no evidence from this standpoint that our two native species belong to different genera.

ASPLENIUM: One of the groups of leptosporangiate ferns which has been most thoroughly investigated is the *Asplenium* group characterized by a basic number of 36. Among its species apogamy is shown by *Asplenium monanthes*, intraspecific euploidy by *A. trichomanes*, and allopolyploidy by *A. ebenoides* and others. In the Appalachian spleenworts, three species that show morphological intermediacy between other species have been found to have 72 pairs at meiosis, supporting a hypothesis of allopolyploidy for these taxa (namely, the Alabama population of *A. ebenoides*, *A. pinnatifidum*, and *A. bradleyi*). Aneuploidy in the *Asplenium* group was suggested for the first time by Britton's report of $n = 35$ for *Camptosorus rhizophyllus* in southern Ontario. However, four populations tested by the author

TABLE II. SUMMARY OF CHROMOSOME NUMBERS REPORTED FOR NORTH AMERICAN FERNS⁵

Ophioglossaceae	<i>n</i>	
<i>Botrychium multifidum</i>	45	(Wagner, 1955)
<i>B. oneidense</i>	45	(Wagner, 1955)
<i>B. dissectum</i> f. <i>obliquum</i>	45	(Britton, '53; Wagner, '55)
<i>B. dissectum</i> f. <i>dissectum</i>	45	(Britton, '53; Wagner, '55)
<i>B. lunaria</i> var. <i>onondagense</i>	ca. 90	(Wagner, '55)
<i>B. simplex</i> var. <i>tenebrosum</i>	45	(Wagner, '55)
<i>B. simplex</i> var. <i>simplex</i>	45	(Wagner, '55)
<i>B. pumicola</i>	45	(Wagner, '55)
<i>B. matricariaefolium</i>	ca. 90	(Wagner, '55)
<i>B. lanceolatum</i> var. <i>angustisegmentum</i>	45	(Wagner, '55)
<i>B. virginianum</i>	92	(Britton, '53; Wagner, '55)
Osmundaceae		
<i>Osmunda regalis</i> var. <i>spectabilis</i>	22	(Britton, '53)
<i>O. cinnamomea</i>	22	(Britton, '53)
"Polypodiaceae"		
<i>Dennstaedtia punctilobula</i>	34 ± 1	(Britton, '53)
<i>Pteridium aquilinum</i> var. <i>latiusculum</i>	52	(Britton, '53)
<i>P. aquilinum</i> var. <i>pseudocaudatum</i>	52	(Wagner, '55)
<i>Pellaea atropurpurea</i>	87	(Manton, '50)
<i>P. glabella</i>	116 ± 2	(Britton, '53)
<i>Adiantum pedatum</i>	29	(Britton, '53)
<i>Pteretis pensylvanica</i>	40 ± 1	(Britton, '53)
<i>Onoclea sensibilis</i>	37	(Britton, '53; Wagner, '55)
<i>Woodsia ilvensis</i>	41 ± 1	(Britton, '53)
<i>Cystopteris bulbifera</i>	42	(Britton, '53; Wagner, '55)
<i>C. fragilis</i>	84	(Britton, '53; Wagner, '55)
<i>C. fragilis</i> var. <i>tennesseensis</i>	126	(Wagner, '55)
<i>C. fragilis</i> var. <i>simulans</i>	84	(Wagner, '55)
<i>C. dickieana</i>	84	(Wagner, '55)
<i>Polystichum acrostichoides</i>	41	(Britton, '53)
<i>Dryopteris spinulosa</i>	82	(Manton & Walker, '53)
<i>D. intermedia</i>	82 ± 1	(Britton, '53)
_____	41	(Manton & Walker, '53)
<i>D. fructuosa</i>	triploid	(Manton & Walker, '53)
<i>D. boottii</i>	unpaired	(Britton, '53)
_____	triploid	(Manton & Walker, '53)
<i>D. marginalis</i>	41	(Britton, '53; Manton & Walker, '53)
<i>D. goldiana</i>	41	(Manton & Walker, '53)
<i>D. cristata</i>	82	(Manton & Walker, '53)
<i>D. clintoniana</i>	123	(Manton & Walker, '53)
<i>Thelypteris phegopteris</i>	90	(Britton, '53)
<i>T. hexagonoptera</i>	30	(Wagner, '55)
<i>T. noveboracensis</i>	29 ± 2	(Britton, '53)
_____	27	(Wagner, '55)
<i>T. palustris</i> var. <i>pubescens</i>	35	(Britton, '53; Wagner, '55)
<i>Athyrium filix-foemina</i> var. <i>michauxii</i>	40	(Britton, '53; Wagner, '55)

⁵ While this paper was in press, I. Manton and W. A. Sledge's paper entitled "Observations on the Cytology and Taxonomy of the Pteridophyte Flora of Ceylon" (Phil. Trans. Roy. Soc. London, Ser. B., Biol. Sci. 238: 127-185, 1954) has appeared, including the following additional cytological records for North America: *Pityrogramma triangularis* (California), *n* = 30; *Adiantum pedatum* (Vancouver), *n* = 29; and *Woodwardia chamissoi* Brack. (California), *n* = 34.

TABLE II.—Continued

<i>A. thelypteroides</i>	40	(Wagner, '55)
<i>A. pycnocarpon</i>	40	(Wagner, '55)
<i>Woodwardia (Anchistea) virginica</i> ..	36 ± 1	(Britton, '53)
.....	35	(Wagner, '55)
<i>W. (Lorinseria) areolata</i>	35	(Wagner, '55)
<i>Asplenium ruta-muraria</i>	72	(Wagner, '55)
<i>A. viride</i>	36	(Britton, '53)
<i>A. trichomanes</i>	36, 72	(Britton, '53)
<i>A. platyneuron</i>	36	(Wagner, '54)
<i>A. bradleyi</i>	72	(Wagner, '54)
<i>A. montanum</i>	36	(Wagner, '54)
<i>A. pinnatifidum</i>	72	(Wagner, '54)
<i>A. trudelli</i>	triploid	(Wagner, '54)
<i>A. ebenoides</i>	(72 univalents)	(Wagner, '54)
..... (Alabama population).....	72	(Wagner, '54)
<i>Phyllitis scolopendrium</i> var. <i>american</i>	72 ± 2	(Britton, '53)
<i>Camptosorus rhizophyllus</i>	35	(Britton, '53)
.....	36	(Wagner, '54)
<i>Polypodium virginianum</i>	37	(Manton, '50)
.....	74	(Britton, '53)

from Ohio, Virginia, and Indiana, showed the usual aspleniaceous number of 36. It should be considered possible that Britton's report was based on an aberrant population; this is a vegetatively reproducing species, and one which might be capable of continued reproduction under abnormal chromosomal conditions. One of the most interesting of the recent findings, mentioned earlier in this paper, was Britton's determination of the chromosome number of the rare limestone-inhabiting American variety of *Phyllitis scolopendrium* as tetraploid, in contrast to the common European representative which is a diploid.

It was worthwhile to find out whether the ill-distinguished American representative of *Asplenium ruta-muraria* (separated by Fernald, without justification in this writer's opinion, as a wholly distinct species, *A. cryptolepis*) might also prove to be distinct cytologically from its European counterpart. The results were negative. Ohio material of this plant showed $n = 72$, as do the European plants (fig. 33).

From the taxonomic viewpoint, it should be emphasized here that the recent reduction by Morton (1952, p. 38) of *A. trudellii* to varietal status under *A. pinnatifidum* has been found to be untenable. This conclusion is based not only on grounds that previously supported its treatment as a hybrid taxon, but on its cytology which also indicated its hybrid nature.

There is a triploid chromosome complement present with approximately 36 pairs and 36 univalents at meiosis (Wagner, 1954, pp. 111-113).

I am more and more inclined to believe that our custom of treating hybrid ferns as binomial taxa (e.g., *Asplenium* × *ebe-noides*, *A.* × *gravesii*, *Dryopteris* × *boottii*, etc.) can be justified on the grounds that follow: (1) Evidently hybridization has played a role in the formation of sexual, allopolyploid species, as well as apogamous species, and these species behave in nature as independent populations with their own separate ranges and ecology, (2) Where the hybrids are sterile, vegetative reproduction may enable them to form large clones of importance in the plant community, not unlike those of the dandelion in cultivated places, and there is some evidence from work now being carried out in this laboratory that forms that lack the capacity to reproduce vegetatively may reproduce (in a manner as yet unexplained) by what appears to be ordinary spore-production, in spite of the fact that the spores are normally abortive and meiosis is highly irregular.

CONCLUSIONS

Forty-eight populations of North American ferns, including 27 species and varieties, were examined cytologically in relation to taxonomic interpretation. The following cytotaxonomic observations are discussed:

1. The subgenus *Osmundopteris* of *Botrychium*, as represented by *B. virginianum*, seems to be the most distinctive, cytologically, of the subgenera, having an apparent basic number of 46 chromosomes and chromosomes of small size.

2. The remaining two subgenera of *Botrychium*, namely *Sceptridium* and *Eubotrychium* appear to be similar to one another cytologically and to possess a base number of 45 chromosomes. Polyploidy has now been observed in *Eubotrychium*.

3. There is no evidence of hybrid origin of *B. oneidense* ($n = 45$). On the contrary, this taxon appears on the basis of chromosomal and other information to behave like a normal species, distinct from both *B. dissectum* ($n = 45$) and *B. multifidum* ($n = 45$), and not like a variety of either of them.

4. In the group of *B. lunaria*, *B. minganense* appears from field studies to be a taxon specifically distinct from *B. lunaria*, although in some respects it appears to be intermediate between the latter species and *B. matricariaefolium*. However, cytological data on *B. minganense* are still not available. *B. lunaria* var. *onondagense* has proved to be a polyploid with $n = \text{ca. } 90$, in contrast to typical *B. lunaria* of Europe, $n = 45$. The related *B. matricariaefolium* is also polyploid ($n = \text{ca. } 90$).

5. Two well-marked varieties of *Botrychium simplex*, the typical variety and var. *tenebrosum*, show no distinctions in chromosome number from each other, and the closely related *B. pumicola* is also indistinguishable (all three with $n = 45$).

6. *Eubotrychium* Sect. *Lanceolatae* as represented by *B. lanceolatum* ssp. *angustisegmentum* ($n = 45$) resembles the species of Sect. *Lunariae*.

7. Further research on the relationship of *Onoclea sensibilis* ($n = 37$) and *Pteretis pensylvanica* ($n = 40$) is suggested by the differences in their chromosome numbers.

8. *Pteridium aquilinum* var. *pseudocaudatum* ($n = 52$) is no different from the other varieties of the bracken thus far studied.

9. A hypothesis of hybridity to explain the "bulblet-bearing" populations of *Cystopteris fragilis* is not directly supported by presently known cytological facts, since *C. fragilis* in Europe and in the United States has not been found to have less than 84 pairs of chromosomes, while *C. bulbifera* has 42. "Bulblet-bearing" plants of *C. fragilis* var. *simulans* show 84 pairs, thus offering no support to an allopolyploid hypothesis. On the other hand, the "bulblet-bearing" *C. fragilis* var. *tennesseensis* yielded $n = 126$, justifying the recent taxonomic separation of these two varieties.

10. The American *Cystopteris dickieana* was found to have $n = 84$ chromosomes like its European counterpart. The only difference (exine sculpture) thus far demonstrated for this taxon does not seem by itself to justify its treatment as a species.

11. The chromosome number of *Thelypteris* (*Phegopteris*) *hexagonoptera* indicates that the base number of the segregate genus *Phegopteris* (formerly in question because the related *T. phegopteris* has $n = 90$ chromosomes and is apogamous) is $n = 30$.

12. *Thelypteris noveboracensis* with $n = 27$ is the lowest-numbered form yet reported for the *Thelypteris* group. The latter group now is known to have a range in chromosome number from 27 to 36, suggesting that either the chromosome numbers in this group tend to fluctuate more readily than in other fern groups, or the group is actually polyphyletic.

13. The species of *Eudryopteris* are well distinguished by their basic chromosome number ($n = 41$) from the thelypteroid ferns, and the evidence that has been accumulated in the past several years shows clearly that hybridization has played a strong role in the evolution of many of the North American populations.

14. There is no reason especially from chromosome number to warrant the placing of *Athyrium pycnocarpon* in a separate genus from *A. thelypteroides* or *A. filix-femina* since all have $n = 40$.

15. Both species of *Woodwardia* of the northeastern United States possess $n = 35$ chromosomes, in contrast to Old World species of *Blechnum* and *Woodwardia*.

16. The ill-defined eastern North American variety of *Asplenium ruta-muraria* with $n = 72$, is indistinguishable in chromosome number from the typical European form.

17. *Asplenium* \times *trudellii* should be considered a hybrid taxon, rather than as a variety of *A. pinnatifidum*, because of its triploid chromosome complement and its meiotic behavior.

18. Our taxonomic custom of treating hybrid ferns as binomials seems justified to this writer in view of their capacity to form populations and behave as typical sexual or asexual plant species.

LITERATURE CITED

- ALSTON, A. H. G. 1951. An overlooked North American fern. *Am. Fern Jour.* **41**: 76-78.
- BRITTON, D. M. 1953. Chromosome studies on ferns. *Am. Jour. Bot.* **40**: 575-583.
- CLAUSEN, R. T. 1938. A monograph of the Ophioglossaceae. *Torr. Bot. Club Mem.* **19** (2): 1-177.
- COPELAND, E. B. 1947. *Genera Filicum*. Waltham, Mass.
- FERNALD, M. L. 1950. *Gray's Manual of Botany*, 8th Edition. American Book Co.
- HOLTUM, R. E. 1946. A revised classification of leptosporangiate ferns. *Jour. Linn. Soc. Bot.* **53**: 123-186.
- MANTON, I. 1950. *Problems of Cytology and Evolution in the Pteridophyta*. Cambridge Univ. Press.
- MANTON, I., and S. WALKER. 1953. Cytology of the *Dryopteris spinulosa* complex in Eastern North America. *Nature* **171**: 1116-1118.
- MORTON, C. V. 1950. Notes on the ferns of the Eastern United States. *Am. Fern Jour.* **40**: 213-225, 241-253.
- . 1952. Pteridophyta, in Gleason, H. A., *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*, pp. 1-56. Lancaster Press.
- NEWCOMER, E. H. 1953. A new cytological and histological fixing fluid. *Science* **118**: 161.
- SELLING, O. H. 1944. Studies in the recent and fossil species of *Schizaea* with particular reference to their spore characteristics. *Meddel. Göteborgs Bot. Trädgård* **16**: 1-112.
- SHAVER, J. M. 1950. A new fern, *Cystopteris tennesseeensis* sp. nov., from Tennessee. *Tennessee Acad. Sci. Jour.* **25** (2): 106-113.
- WAGNER, W. H. 1944. Another occurrence of the apparent hybrid *Cystopteris*. *Am. Fern Jour.* **34**: 125-127.
- . 1954. Reticulate evolution in Appalachian *Aspleniums*. *Evolution* **8**: 103-118.
- WEATHERBY, C. A. 1935. A new variety of *Cystopteris fragilis* and some old ones. *Rhodora* **37**: 374-378.
- WHERRY, E. T. 1944. *Cystopteris* Bluff. *Am. Fern Jour.* **34**: 92-94.

Volume 57, no. 679, including pages 189-212, was issued 2 August, 1955.